

Relationships of Cretaceous Ripiphoridae (Coleoptera) based on larval morphology, with evidence for the same reproduction timing and chosen microhabitat for oviposition

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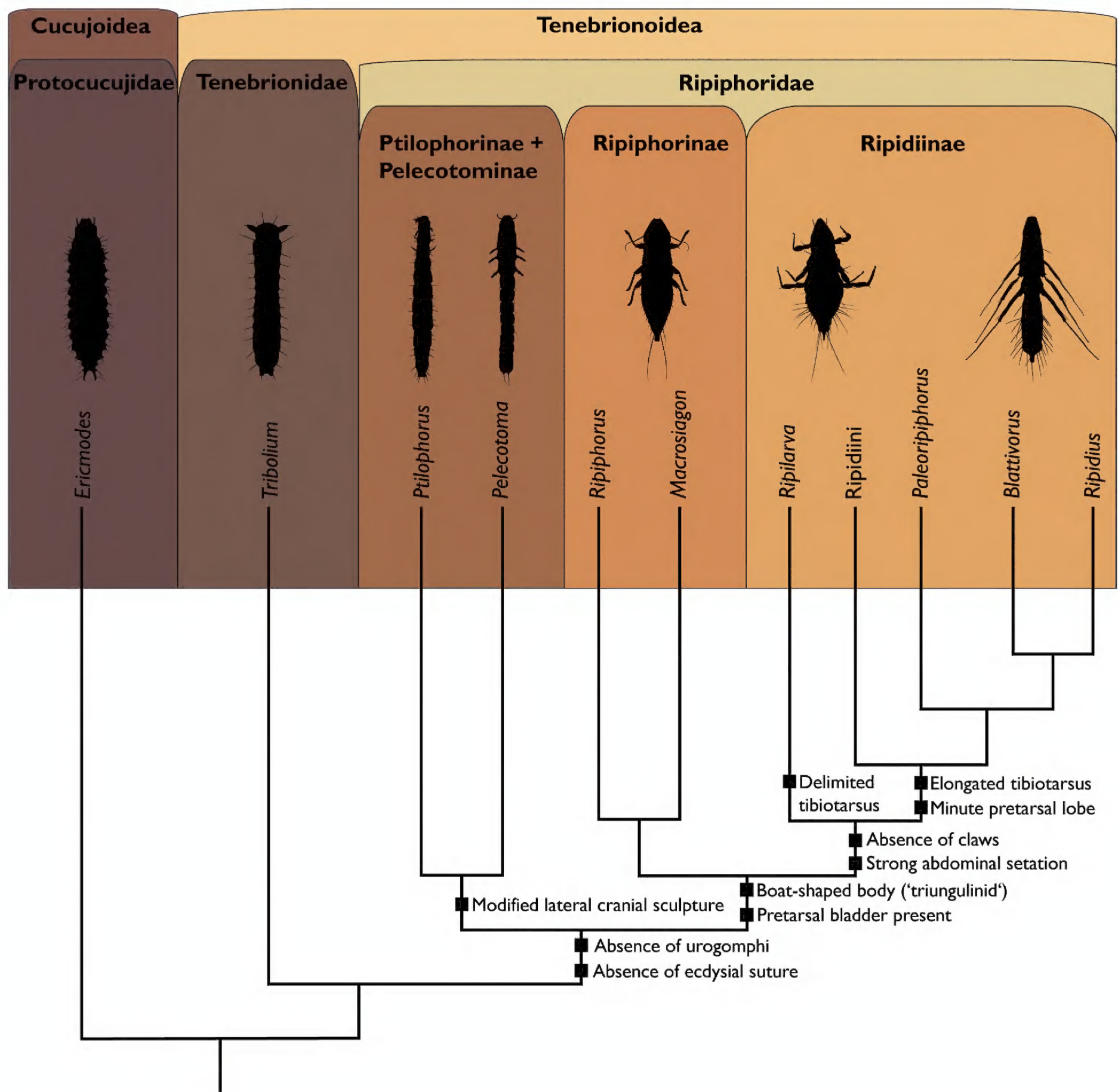
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Abstract

Five specimens of primary larvae of Ripiphoridae (Insecta: Coleoptera) are reported from one piece of Cretaceous Kachin amber. They represent two morphotypes: one conicocephalate and one belonging to the tribe Ripidiini (represented by four specimens). The conicocephalate morphotype is compared with similar larvae known from Kachin, Taimyr and Manitoba Cretaceous amber, and the larvae of Ripidiini are compared with their Cretaceous, Eocene and extant relatives. Phylogenetic analyses were performed to establish a working hypothesis about possible relationships of both lineages. The results, which conform with a recent molecular phylogeny, indicate that the larvae described here belong to Ripidiini or are closely related, respectively. To allow taxonomic and systematic work with conicocephalate larvae from Kachin amber, a collective group name †“*Ripilarva*” **nov.** is proposed here to accommodate these immature stages. Both species of †“*Ripilarva*” **nov.** from Kachin amber are described: †“*R.*” *parabolica* **sp. nov.** and †“*R.*” *kachinensis* **sp. nov.** Syninclusion of †“*Ripilarva*” *kachinensis* **sp. nov.** and four larvae of a species of Ripidiini indicate that females of both ripiphorids chose the same time and microhabitat for oviposition in the Kachin Cretaceous forest. The results are further verified by the use of UV-photography, as the different larval morphotypes occurred in the same resin flow. The presence of larvae of Ripidiini in clusters contrary to the solitary occurrence of †“*Ripilarva*” **nov.** in Cretaceous amber of Russia, Canada, USA, and Myanmar is interpreted as a possible result of different oviposition strategies, with different numbers of eggs deposited at one spot.

Graphical abstract



Key Words

Apomorphies, Burmite, fossil, parasite, phenology, phylogeny, syninclusions, wedge-shaped beetles

Introduction

Fossils of various ages can not only illuminate the morphology and early phylogeny of the groups in question, as for instance in the case of different members of the stem group of Strepsiptera (Pohl and Beutel 2016; Pohl et al. 2021), but also provide deep glimpses into the evolution of taxa, concerning for instance the preferred microhabitats, and also developmental and life strategies. A

recent study on a stem group ant embedded in Burmite, †*Gerontoformica*, yielded a direct proof of eusociality in Formicidae in the mid-Cretaceous (Boudinot et al. 2022). Similarly, the discovery of minute primary larvae of Strepsiptera in Burmese amber demonstrated that endoparasitism was already established in this group about 100 million years ago (Pohl et al. 2018). Small myxophagous beetles of †*Triamixidae*, found in abundance in Triassic coprolites of small dinosaurs, revealed that they

were likely living among aquatic plants in the early Mesozoic, and were ingested in large numbers by amphibious vertebrates (Qvarnström et al. 2021). Syninclusions preserved in amber of various ages document extraordinary interactions of insects with plants, for instance beetles with orchid pollinaria (Poinar 2016), or also swarming and mating behavior (Arillo 2007). As the term syninclusion is rather unspecific, biological specimens included in one piece of amber should rather be categorized by their position together in the same resin flow, i.e., eusyninclusion, or in a different one, i.e., parasyninclusion (Solórzano-Kraemer et al. 2023). Adopting this categorization makes more precise conclusions on the ecology of extinct organisms possible (Solórzano-Kraemer et al. 2023), as individuals in the same resin flow could indicate an ecologically meaningful relationship, for instance in the context of parasitism (Luo et al. 2023) or predation (Barden et al. 2020). The present case of two distinctive types of ripiphorid primary larvae in a single piece of amber prompts speculations about different reproductive strategies, which may have evolved in this unusual and specialized group of cucujiform Coleoptera. The concepts of eu- and parasyninclusions (Solórzano-Kraemer et al. 2023) are applied for the first time for extinct insect parasites.

Within the last two decades, the Ripidiinae of the cucujiform parasitic beetle family Ripiphoridae has become a well-studied group in the Cretaceous fossil record. Five new genera were described based on males from France and Myanmar amber (Perrichot et al. 2004; Falin and Engel 2010; Batelka et al. 2018; Cai et al. 2018; Batelka and Prokop 2019). Longipedes larvae were identified as primary larvae of Ripidiinae in Myanmar and New Jersey amber (Batelka et al. 2019) and subsequently identified as †*Paleoripiphorus* Perrichot, Nel & Néraudeau, 2004, originally described based on a male from France (Batelka et al. 2021a). Simultaneously, the first fossil female of Ripidiini ever described was discovered in association with †*Paleoripiphorus* males and primary larvae of the same species. Based on this extraordinary syninclusion with 28 males, one female and two larvae, and due to the complex biology of this species, the hypothesis on aggregative behaviour of Ripidiinae males documented in Cretaceous, Eocene, and Miocene amber was reformulated. A gradual accumulation of males over a longer time span was suggested, as a result of sexual communication with sedentary and larviform females (Batelka et al. 2021a). The distribution of this genus in various types of Cretaceous amber has revealed †*Paleoripiphorus* as an important insect element of the Laurasia supercontinent, covering a time span of 30 My from the uppermost Albian amber of France to Turonian amber of New Jersey.

In contrast to Ripidiinae, information about the so-called “conicocephalate” larvae (term introduced by Kathirithamby et al. (2017)) is scarce. A single specimen discovered in Cretaceous amber of Manitoba (Canada) was described as a putative triungulinid (i.e., primary larva) of Strepsiptera by Grimaldi et al. (2005). A similar specimen was described from Kachin amber by Beutel et al. (2016) and interpreted as a beetle larva, likely of the

family Ripiphoridae. In response to this, Kathirithamby et al. (2017) described another specimen from Cretaceous amber of Taimyr, again as a first instar of Strepsiptera. Because of the discovery of an unquestionable primary strepsipteran larva in Kachin amber (Pohl et al. 2018) and morphological comparative analyses performed by Batelka et al. (2019, 2020), we adopt the interpretation of Beutel et al. (2016) that these larvae likely belong to Ripiphoridae. However, nothing is presently known about the systematic position or biology of these unusual immature stages, except for a hypothesis about possible adaptation of their legs for phoresy (Batelka et al. 2018).

Here we present the discovery of four specimens of unknown primary larvae of an unidentified genus of Ripidiini and one new conicocephalate larva, preserved together in one piece of Kachin amber. We provide descriptions of both morphotypes and compare them with other related species. The results are tested phylogenetically and discussed in the context of the evolution of the family. We also discuss the putative importance of this syninclusion for the interpretation of the biology and simultaneous and syntopical occurrence of both groups in a Cretaceous forest.

Material and methods

Material

This study is based on arthropod inclusions preserved in a mid-Cretaceous piece of amber from Hukawng Valley, Kachin, northern Myanmar. The size of the piece is 2.4 × 1.5 cm (longest distances taken). All five specimens of larvae of both ripiphorid species are numbered R1–R5 (Figs 1–3): R1 = conicocephalate larva, R2–R5 = Ripidiini larvae (R2 isolated specimen, R3 and R4 (the slightly curved and shrunken specimen) close to each other, and R5 (isolated specimen with partly missing tergites) preserved at the opposite edge of the amber). Syninclusions belong to Acari, Collembola, Psocodea and an unidentified nymph of a hemimetabolous insect. For all specimens we have adopted the combination of the amber piece code PMJ Pa 6100 and the specific subcode of the individual R1–R5, Ps, Ac1–Ac4, Ny or Co.

The barklouse (Figs 1, 3, Ps; PMJ Pa 6100-Ps) can be assigned to the family Compsocidae and genus †*Burmacompsocus* as defined by Nel and Waller (2007) and Álvarez-Parra et al. (2023) of the suborder Troctomorpha. Using the description and information provided by Nel and Waller (2007), Sroka and Nel (2017) and Ngô-Muller et al. (2020), we could identify it as belonging to either the species †*Burmacompsocus perreai* Nel & Waller, 2007 or †*Burmacompsocus pouilloni* Ngô-Muller, Garrouste & Nel, 2020. The specimen displays several specific features of the forewing fitting with the descriptions of both species, the short cross-vein between Rs and M, the long M vein branches, and the separation of veins A1 and A2. The slightly lower area between R2+3 and R4+5 as well as between M2+M3, and the position of the apex of Rs distad of

the half length of the pterostigma is in stronger agreement with the description of †*B. perreaui*. It differs distinctly from †*Burmacompsocus conjugans* Sroka & Nel, 2017 by the longer M veins and the cross vein rs-m on the forewing. Body length: 1.6 mm. Forewing length: 1.8 mm. Hindwing length: 1.5 mm. The length measurements of the wings are similar to the ones of †*B. pouilloni*, while the specimen is smaller than described for †*B. perreaui*. Due to a low amount of specimen sampling and fragmentary species descriptions, it is presently not clear, if both species, †*B. perreaui* and †*B. pouilloni* are two distinct species, as they mainly differ in two ratios of the forewing.

As previously discussed by Mockford et al. (2013), †*B. perreaui* shares a highly similar wing venation with †*Burmacompsocus banksi* (Cockerell, 1916). Due to the poor preservation of the holotype of †*B. banksi* (Cockerell, 1916) its taxonomic status is currently unclear. It might either represent a unique species, or †*B. perreaui* is a synonym of this species (Azar et al. 2016). Another species, †*Burmacompsocus ojancono* Álvarez-Parra & Nel, 2023, is described from Cretaceous Spanish amber (Álvarez-Parra et al. 2023).

There are also four mites included in the amber piece (Figs 1, 4, Ac1–Ac4). One individual likely belongs to the Oribatida (Figs 1, 4, Ac2; PMJ Pa 6100-Ac2), while two specimens are nymphs (possibly 2nd instars) (Figs 1, 4, Ac3, Ac4; PMJ Pa 6100-Ac3, PMJ Pa 6100-Ac4) of Erythraeidae (J. Dunlop, pers. comm.). One single mite could not be identified but could possibly also belong to Erythraeidae (Fig. 1, 4, Ac1; PMJ Pa 6100-Ac1). Additionally, one specimen of Collembola (Figs 1, 4, Co*; PMJ Pa 6100-Co), presumably with entomobryomorphan affinities, is included, close to the posterior side of the psocid. Unfortunately, the inclusion is not well preserved, and it is not possible to observe any more details. Furthermore, one inclusion that likely represents a nymphal stage of a hemimetabolous insects (Figs 1, 4, Ny; PMJ Pa 6100-Ny) is located close to the conicocephalate larva.

The amber specimen is stored in the Phyletisches Museum, belonging to the Friedrich-Schiller-Universität Jena (Jena, Germany), under the entrance number 23/023, cataloging number PMJ Pa 6100 and the collection number of MW BuA_MW_0001.

Specimen preparation

The amber piece was polished in several successive steps, using wet Starcke abrasive paper (Starcke, Melle, Germany). Flattening and thinning the piece was done with abrasive paper ST400, and the surface was successively polished with ST1200, ST2000, ST3000, ST5000, and ST7000. Finally, lime powder was used to remove minute scratches.

Imaging

All photographs were developed in Adobe Lightroom classic (v.11.5) (Adobe, San Jose, USA). Single images

were denoised (option: standard) with Topaz DeNoise AI (Topaz Labs, Dallas, USA) and merged with Zerene stacker 1.04 (Zerene System LLC, Richland, USA). All plates were compiled using Adobe Photoshop (v. 24.1.0) and Adobe Illustrator (v. 27.2) (Adobe, San Jose, USA).

An overview image was taken through partially focused stacks with a Canon EOS R5 equipped with a Canon EF 100mm f/2.8L Macro IS USM (Canon, Krefeld, Germany). For stacks the focus bracketing software of the camera was used. The camera was mounted on a Kaiser copy stand. The specimen was illuminated with a Euromex LE.5211-230 cold light source (Euromex, Papenkamp, Netherlands) with three gooseneck lamps. The amber piece was placed in a clear glass petri dish filled with distilled water to prevent any damage to the object, as suggested by Sadowski et al. (2021).

Detail photos were taken at the Museum für Naturkunde Berlin with a Zeiss Axioscope 5 (Carl Zeiss AG, Oberkochen, Germany), mounted with a Canon EOS 80D (Canon, Krefeld, Germany) via a T2-T2 1,6× SLR tube. Stacks were taken manually.

Additional images of syninclusions were taken with a Canon EOS R5 (Canon, Krefeld, Germany) mounted with a Micro-Tube M26 (Novoflex, Memmingen, Germany) and equipped with a five times magnification microscope objective M Plan Apo (Mitutoyo, Kawasaki, Japan). Stack shots were realized with a StackShot macro rail (Cognisys, Traverse City, MI, USA) that were afterwards combined with Zerene Stacker ((Zerene Systems LLC, Richland, WA, USA). For stable positioning of the amber piece, it was placed in Balea Hygiene Handgel (Dalli GmbH & Co. KG, Stolberg (Rhld.), Nordrhein-Westfalen) (Septigel) within a petri dish (Weingardt et al. 2023), with a cover slip on top. To achieve an evenly illumination the whole petri dish was covered with a plastic dome (Rayher, Laupheim, Germany), which was grinded with abrasive paper (Starcke, Melle, Germany) and colored with white (RAL 9010) spray paint (Maston, Veikkola, Finland). The specimens were illuminated with two flashlights (Phottix Juno Li60 Flash, New York, USA) controlled with two Yongnuo RF603C II wireless triggers (Yongnuo, Shenzhen, China). After taking photographs the amber piece was rinsed and cleaned under running water.

UV-Photography

Stacked UV-images of amber were made using the same settings as for other pictures. For images (Fig. 4A–D) a LepiLED with a wavelength of 368 nm (<https://www.gunnarbrehm.de/lepi-led>) was used. For fixation of the lamp and amber, we used white FIMO® as it does not fluoresce under UV light, to prevent artifacts in the photographs. For Fig. 5 (A–D) two paired UV-LEDs (368 nm) were held diagonally above the amber with a distance of ca. 30 cm. This generates an opaquer image with a better visibility of the resin layers (flows).

Comparative taxonomy

For comparative analysis and differential diagnosis of the Ripidiini species, we refer to descriptions of the following primary larvae of the tribe: *Blattivorus inquirendus* (Silvestri) (Silvestri 1906); †*Paleoripiphorus* Perrichot, Nel & Néraudeau, 2004 (Batelka et al. 2019); *Ripidius quadriceps* Abelle de Perrin (Besuchet 1956); and †*Ripidius* sp. from Eocene amber (Batelka et al. 2020).

Analytical methods

A matrix with 19 characters (all unweighted and unordered) scored for 14 terminal taxa was used in the phylogenetic analysis. The parsimony analyses were carried out with NONA (ratchet, 1000 replicates) (Goloboff 1995), and also with TNT (traditional search) (Goloboff et al. 2008), also using the implied weighing option ($K = 3.000$). Branch support values (Bremer 1994) were calculated with NONA. Finally the trees were redrawn in Adobe Illustrator (v. 27.2) (Adobe, San Jose, USA).

Outgroup taxa: *Ericmodes* sp. (Protocucujidae), *Tribolium* sp. (Tenebrionidae); Ripiphoridae (12 taxa): *Pelecotoma fennica* (Pelecotominae), *Ptilophorus dufourii* (Ptilophorinae), †*Paleoripiphorus* sp., Cretaceous †Ripidiini Gen. sp., *Blattivorus inquirendus*, *Ripidius quadriceps* (Ripidiinae), *Ripiphorus smithi*, *Macrosiagon ferruginea* (Ripiphorinae), †“*Ripilarva*” *parabolica*, †“*Ripilarva*” *kachinensis*, †“*Ripilarva*” from Taymir, †“*Ripilarva*” from Manitoba (genus and subfamily *incertae sedis*). Data for *Ericmodes* were taken from Beutel and Ślipiński (2001) and Ślipiński and Beutel (2010).

All of the image data and the character matrix are available from MorphoBank via <http://morphobank.org/permalink/?P5334>.

Characters of primary larvae of Ripiphoridae with potential phylogenetic significance

1. Habitus: (0) non-triungulinid, approximately parallel-sided body (*Ericmodes*, *Tribolium*, Pelecotominae, Ptilophorinae); (1) triungulinid, boat-shaped body (Ripiphorinae, Ripidiinae, †“*Ripilarva*”).
2. Head: (0) subglobular (*Ericmodes*, *Tribolium*); (1) flattened, bell-shaped, rounded anteriorly (Ripiphorinae, Ripidiinae, †“*Ripilarva*” *parabolica*); (2) triangular and anteriorly pointed (†“*Ripilarva*” spp. excl. †“*R.*” *parabolica*); (3) flattened, parallel-sided and elongated (Pelecotominae, Ptilophorinae). The triangular anteriorly pointed head is a highly unusual derived condition.
3. Dorsal ecdysial suture of head: (0) present (*Ericmodes*, *Tribolium*); (1) absent (Ripiphoridae). The absence is likely a groundplan apomorphy of the family (Švácha 1994; Lawrence et al. 2010).
4. Lateral cranial area: (0) with scale-like sculpture (Pelecotominae, Ptilophorinae); (1) smooth (all remaining genera).

5. Eyes: (0) several stemmata (*Ericmodes*, *Tribolium*, Pelecotominae, Ripiphorinae, extant Ripidiinae); (1) stemmata absent (Ptilophorinae, †“*Ripilarva*”). Separate stemmata belong to the groundplan of the family (e.g., Lawrence et al. 2010). Eyes are indiscernible in fossil Ripidiinae as the inclusions are translucent.
6. Antennal insertion: (0) anterolaterally (*Ericmodes*, *Tribolium*, Pelecotominae, Ptilophorinae); (1) posterolaterally (Ripiphorinae, Ripidiinae pars.). Not applicable in †“*Ripilarva*” and †*Paleoripiphorus*. The posterior shift of the antennal insertion is an unusual apomorphic condition of a large subgroup of the family.
7. Antennal sensorium: (0) large, cone-shaped (*Ericmodes*, *Tribolium*, Pelecotominae, Ptilophorinae); (1) short, spiniform (Ripiphorinae); (2) long, bristle-like (*Ripidius*, *Blattivorus*). Not applicable in †“*Ripilarva*” and †*Paleoripiphorus*.
8. Ctenidia: (0) present (†“*Ripilarva*”, †*Paleoripiphorus*); (1) absent (all remaining genera). The presence of ctenidia on the ventral side is a highly unusual apomorphic condition. This is unknown in larvae of extant species of the family.
9. Shape of meso- and metanotum: (0) parallel sided (*Ericmodes*, *Tribolium*, Pelecotominae, Ptilophorinae); (1) distinctly widening posteriorly (all remaining genera).
10. Tibiotarsus: (0) short and robust (*Ericmodes*, *Tribolium*, Pelecotominae, Ptilophorinae, Ripiphorinae, †“*Ripilarva*”); (1) distinctly elongated and extremely thin (Ripidiinae).
11. Claws: (0) absent (†“*Ripilarva*”, †*Paleoripiphorus*, Cretaceous †Ripidiini gen. sp.); (1) present (all extant ripiphorids, *Ericmodes*, *Tribolium*). A single claw is present in the groundplan of the family (Švácha 1994) and also occurs within extant Ripidiinae and Ripiphorinae (e.g., Lawrence et al. 2010). The absence in all known Cretaceous larvae is clearly a derived condition.
12. Unpaired pretarsal adhesive lobe (bladder): (0) absent (*Ericmodes*, *Tribolium*, Pelecotominae, Ptilophorinae); (1) present (Ripidiinae, Ripiphorinae, †“*Ripilarva*”). This flexible, lobe-like attachment structure, very similar to the one of strepsipteran larvae (Pohl and Beutel 2004), is likely an apomorphy of Ripiphoridae excl. Pelecotominae and Ptilophorinae. The presence in two non-related parasitic groups shows that this is very likely related with the necessity to attach efficiently to the cuticle of an insect host.
13. Size of pretarsal lobe: (0) minute (Ripidiinae), (1) large (Ripiphorinae, †“*Ripilarva*”). Not applicable for *Ericmodes*, *Tribolium*, Pelecotominae and Ptilophorinae.
14. Tibiotarsus: (0) delimitation of tibia and tarsus discernible (†“*Ripilarva*”); (1) border between tibia and tarsus indiscernible (all remaining taxa).
15. Shape of abdomen: (0) parallel-sided or subparallel (*Ericmodes*, *Tribolium*, Pelecotominae, Ptilophorinae); (1) widest in the area of segment 2, then

continuously narrowing towards the abdominal apex (all remaining taxa). A parallel-sided or subparallel abdomen belongs to the groundplan of the order (e.g., Lawrence et al. 2010). An abdomen with broad segments I–II and then narrowing continuously is likely synapomorphy of the respective taxa.

16. Abdominal spiracles: (0) eight (*Ericmodes*, *Tribolium*, Ptilophorinae); (1) seven (Ripiphorinae); (2) less than seven (Pelecotominae, *Blattivorus*, *Ripidius*). Unknown in fossil Ripidiinae and †“*Ripilarva*”.
17. Concentration of very long setae on abdominal segments: (0) absent (*Ericmodes*, *Tribolium*, Pelecotominae, Ptilophorinae, Ripiphorinae); (1) present (Ripidiinae, †“*Ripilarva*”).
18. Segment X (pygopodium): (0) short and broad sucker, used for locomotion (*Ericmodes*, Pelecotominae, Ptilophorinae, Ripiphorinae); (1) elongate and tube-like (*Ripidius*, *Blattivorus*, †“*Ripilarva*” spp. except the one from Taymir); (2) rounded (†*Paleoripiphorus*, †“*Ripilarva*” from Taymir, Cretaceous Ripidiini gen. sp.); (3) paired pygopods (*Tribolium*).
19. Urogomphi on segment IX: (0) present (*Ericmodes*, *Tribolium*); (1) absent (Ripiphoridae).

Results

Systematic palaeontology

Ripiphoridae, subfamily *incertae sedis* Ripidiinae, tentative placement

Holometabolan larva of triungulinid morphotype (Beutel et al. 2016), known only in Ripiphoridae and Strepsiptera. From triungulin larvae of some Meloidae (Coleoptera) it differs mainly by the presence of a pretarsal pad, from Strepsiptera by abdominal segments widening posteriorly and a different placement of the terminal bristles. For discussion of other characters see Beutel et al. (2016), Batelka et al. (2019, 2020), and Pohl et al. (2018).

†“*Ripilarva*” Batelka & Beutel, nov.

Note 1. The quotation marks for “*Ripilarva*” indicate here its status as collective group name.

Diagnosis. First instar of parasitic larva. Body small, 0.34–0.56 mm long (excluding terminal bristles), boat-shaped, strongly flattened. Head triangular or parabolic, as long as pronotum or shorter, with one or more ventral straight ctenidia; mandibles simple (indiscernible in some specimens), antennae and palpi in most specimens indiscernible, short and bristle like if visible, and stemmata indiscernible. Thoracic segments with posteroventral ctenidia (synapomorphy of the group), overlapping each other slightly, width of segments increasing from prothorax to metathorax; meso- and metathorax distinctly widening posteriorly. Length of head + pronotum versus

mesonotum + metanotum about 0.7–0.9 : 1. Coxae distinctly protruding beyond thoracic segments, trochanter not recognizable; femur broad, tibia and tarsus distinguishable (in contrast to typical tibiotarsus in Polyphaga), not flagellate as in Ripidiinae; pretarsus with soft, unpaired, pad-like appendage, lacking claws. Legs in all known specimens distinctly bent towards head (taphonomic character likely caused by muscle contractions). Abdomen widest at segment II or III, remaining segments strongly tapering towards apex; all segments with concentration of long bristle-like setae, two caudal bristles are the longest (sometimes longer than abdomen).

Note 2. A collective group name (ICZN 1999) is established here to accommodate conicocephalate larvae, a term introduced by Kathirithamby et al. (2017) and adopted for instance by Batelka et al. (2019, 2020) for larvae of a similar morphotype reported so far from Cretaceous amber of Canada, Myanmar and Russia. As the larvae from Canada and Russia are so far unique for the respective deposits, assigning them a species name is not necessary for the time being. Here we provide species names only for both larvae from Kachin amber to distinguish them formally in this contribution.

No type species is designated in accordance with the article 13.3.2. of ICZN (1999). See also articles 42.2.1., 42.3.1 and 66 ibidem.

Etymology. Composed from Ripi – (first part of the family name) and larva (indicating its immature nature). Feminine gender. The name is registered under ZooBank LSID <https://zoobank.org/02E6F710-27C8-40B4-8D8F-52B0700D0CF6>.

†“*Ripilarva*” *kachinensis* Batelka & Beutel, sp. nov.

<https://zoobank.org/A27442B4-0F9D-4111-A85E-273BA6F891B3>

Figs 1, 2, 5, 6, R1

Holotype. PMJ Pa 6100 (collection number of MW BuA_MW_0001) stored in the Phyletisches Museum, Friedrich-Schiller-Universität Jena (Jena, Germany), specimen R1.

Description. Habitus. Small, about 0.56 mm excluding terminal bristles. Well sclerotized on dorsal side, with partially translucent cuticle on head and thoracic nota. Coloration of anterior body from dark yellow to dark brown, but abdominal segments apparently very dark. Vestiture of long setae present, but largely restricted to abdomen. Head with distinctly visible row of apically rounded spines (ctenidium) on ventral posterior margin. Thorax distinctly longer than abdomen, with meso- and metathorax distinctly widening posteriorly. Legs strongly developed; unpaired pretarsal adhesive lobes unsclerotised and translucent; all six tibiotarsi oriented towards head. Abdomen 10-segmented, widest in anterior third and very distinctly narrowing towards apex; with pair of long terminal bristles and tubular terminal segment.

Head. Shape equilateral triangular; short, ca. 0.1 mm from mandibles to posterior margin in dorsal view and ca. 0.1 mm broad posteriorly. Mouth opening discernible.

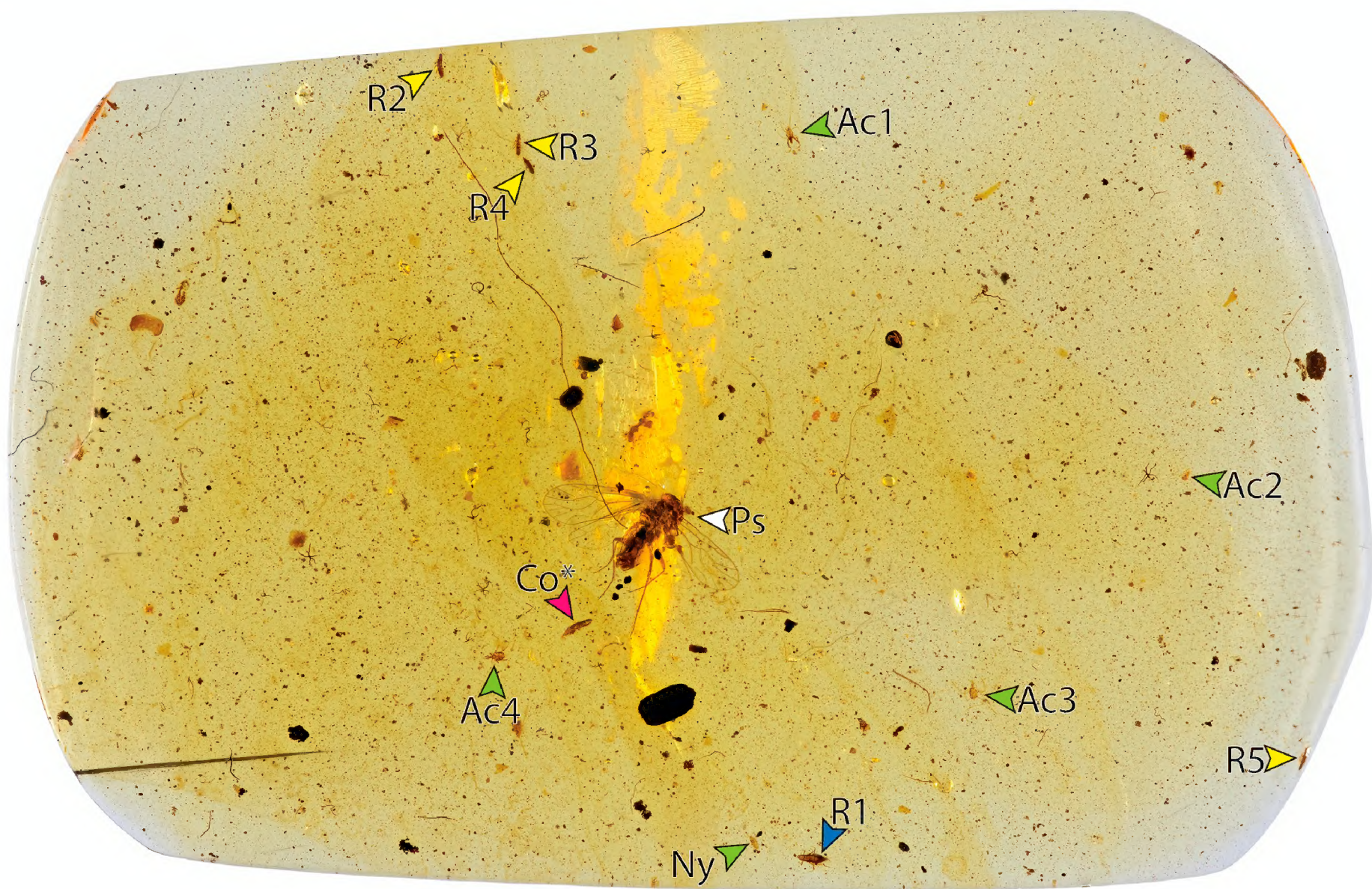


Figure 1. Kachin amber piece containing Ripiphoridae larvae. R1 = Holotype of †“*Ripilarva*” *kachinensis* sp. nov., R2–R5 = Ripidiini larvae, Ac1 = unidentified mite, Ac2 = Oribatida, Ac3–4 = Erythraeidae immatures, Co* = entomobryomorphan Collembola (?), Ny = hemimetabolous nymph, Ps = Psocodea (Compsocidae). Scale bar: 1 cm.

Mandibles scarcely visible. Possible terminal palpomere and bristle-like terminal seta of maxillary palpus projecting on both sides of head. Cephalic setae absent. Labrum and clypeus not recognisable as separate structures or regions. Epicranial sutures absent. Stemmata lacking or at least not discernible. Posterodorsal margin of head capsule recognisable by darker coloration. Head without any scale- or lobe-like posterolateral extensions. Mouthparts, sutures, ridges or gula not recognizable on ventral side. Tentorium or tentorial grooves not visible, presumably absent. Posteroventral edge with medially concave regular row of 12 or 14 flattened, short and apically rounded spines, forming ctenidia, each less than 10 µm long.

Thorax. Large, about half of total body length. All three segments subequal in length; meso- and metathorax distinctly widening posteriorly, maximum width of segments increasing from anterior to posterior. **Prothorax** with well-developed pronotum with wide median ecdysial line and rounded lateral margin; maximum width at posterior third; one strongly developed and long seta (ca. 30 µm) inserted on posterolateral corner; ventral side without recognizable sternal plate; ctenidium similar to that on head, partially recognisable. Forelegs with relatively short parallel-sided coxa distinctly protruding beyond lateral pronotal margin, with two opposite bristle-like setae in distal corners; trochanter not recognizable like on middle and hind legs; femur moderately

sized, ca. 50 µm long, fairly broad, with almost straight anterior margin and distinctly convex posterior margin; distal segment composed of tibia and tarsus (fused but of distinct widths, forming tibiotarsus) very slender; claws missing but apical unpaired pad-like adhesive device present (erroneously addressed as pulvillus in some previous studies). **Mesothorax** slightly longer than prothorax, with wide median ecdysial line, and with distinctly widened and rounded posterolateral corners and long posterolateral seta. Mesonotum simple, without any differentiation or recognisable subdivision; ctenidium partially recognisable, similar to that on head. Middle legs with elongated, cylindrical, apically slightly widening coxa extending far beyond lateral mesonotal margin; mesofemur longer and slightly narrower than profemur; distal elements very similar those of proleg. **Metathorax** very similar in shape to mesothorax, but slightly shorter and slightly broader. Metanotum simple, with pair of setae close to hind margin, inserted relatively distant from lateral margin; very long seta inserted posterolaterally on ventral side of segment; ctenidium not recognisable. Hind legs distinctly longer than forelegs and middle legs, very prominent; metacoxae also elongate and cylindrical; metafemur and distal elements slightly larger than those of anterior pairs of legs.

Abdomen. Ten-segmented, shorter than thorax (ca. 0.19 mm). All terga simple and sclerotized, those of

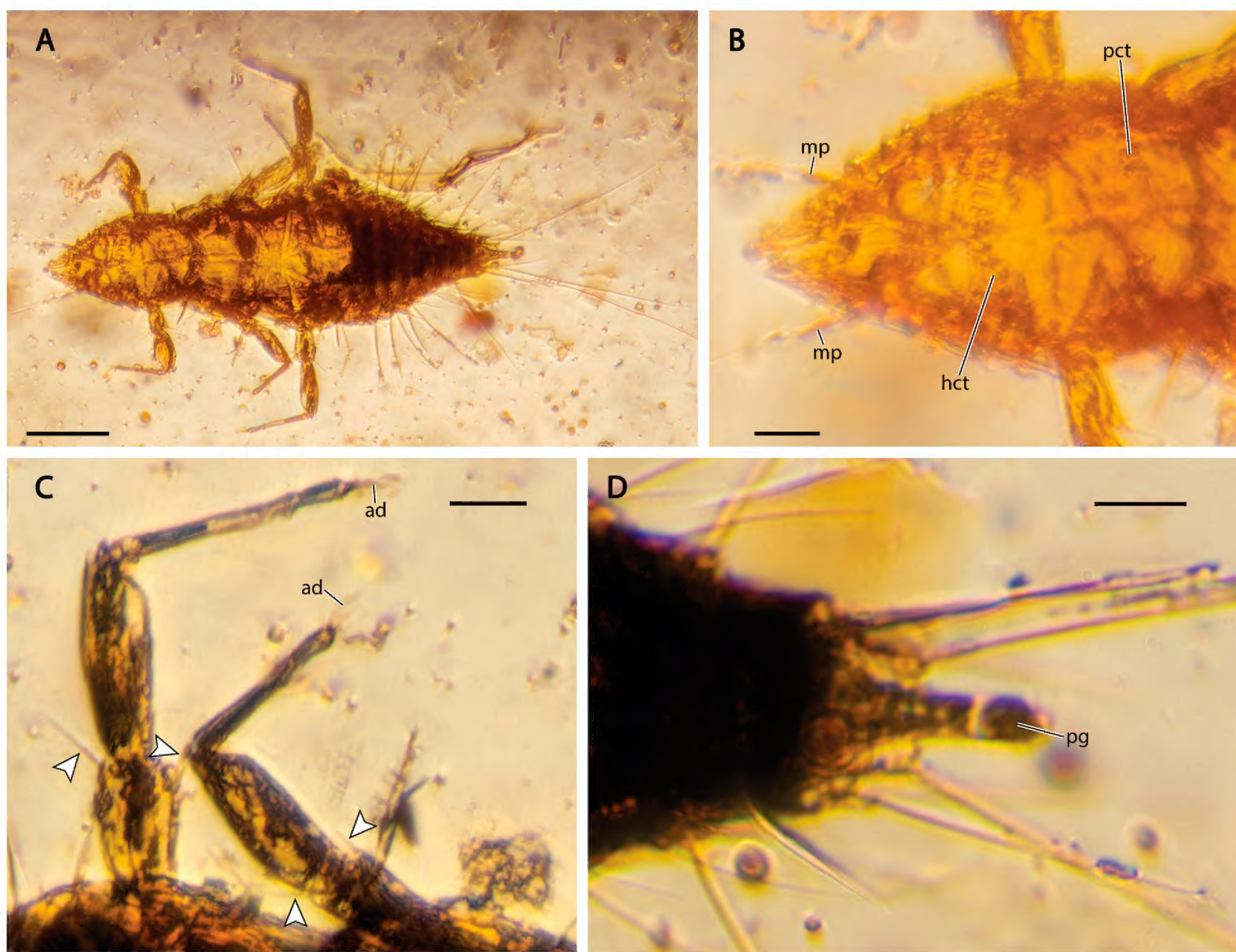


Figure 2. Detailed views of taxonomically important characters of holotype of †‘*Ripilarva*’ *kachinensis* sp. nov. [R1]. **A.** General overview of larva [dorsal]; **B.** Details of head; **C.** Details of legs; **D.** Details of postabdomen. ad = adhesive devices, hct = head ctenidium (segment X), mp = maxillary palps, pct = prothoracic ctenidium, pg = pygopod. Arrows in **C** indicate coxal setae. Scale bars: 100 μ m (**A**); 25 μ m (**B–D**).

segments I–VIII with straight posterior margin; greatest width at segment II, strongly tapering towards apex. Segments II–VIII bearing long lateral setae. Segment I relatively long, widening posteriorly. Segments II–IV shorter, almost parallel-sided, III distinctly narrower than II, and IV narrower than III. Segments V–VIII slightly longer, each of them narrower than the preceding one. Segment IX about twice as wide as long, with rounded posterior margin and posterolaterally inserted caudal bristles distinctly longer than entire abdomen (0.24 mm). Segment X narrow, tubular. Spiracles not recognizable.

Differential diagnosis: †‘*Ripilarva*’ *kachinensis* sp. nov. differs from †‘*Ripilarva*’ *parabolica* sp. nov. illustrated in Beutel et al. (2016) by the distinctly triangular head. Other differences are inconspicuous or uncertain. The putative absence of the metathoracic ctenidium and the longer abdominal segment X might be due to imperfect or different preservation of both fossils and observation constrains. †‘*Ripilarva*’ sp. from Manitoba and †‘*Ripilarva*’ sp. from Taimyr have two rows of ctenidia on the head. The anterior ctenidium is not visible in †‘*Ripilarva*’ *kachinensis* sp. nov. and possibly missing.

Etymology. The species name refers to place of origin of the Kachin amber.

†‘*Ripilarva*’ *parabolica* Batelka & Beutel, sp. nov.

<https://zoobank.org/2A586114-6527-4DEC-8043-A963DECA6BC2>

Holotype. NO. BU-001009. Presently in the collection of the Institute of Zoology of the Chinese Academy of Sciences in Beijing (Prof. Dr. BAI Ming). The specimen will eventually be deposited in the Three Gorges Entomological Museum, Chongqing, China.

Description. Beutel et al. (2016).

Differential diagnosis. †‘*Ripilarva*’ *parabolica* differs from †‘*Ripilarva*’ *kachinensis* by its parabolic head which is not pointed anteriorly.

Etymology. The species name refers to the parabolic shape of the head.

List of conicocephalate larvae included in the †‘*Ripilarva*’ Batelka & Beutel, nov.

†‘*Ripilarva*’ *kachinensis* Batelka & Beutel, sp. nov. (Myanmar; this study)

†‘*Ripilarva*’ *parabolica* Batelka & Beutel, sp. nov. (Myanmar; Beutel et al. 2016)

†‘*Ripilarva*’ sp. (Manitoba, Canada; Grimaldi et al. 2005)

†‘*Ripilarva*’ sp. (Taimyr, Russia; Kathirithamby et al. 2017)

†*Ripidiini* gen. et sp. indet.

Figs 1, 3, 5, 6, R2–R5

Material. Primary larvae PMJ Pa 6100 (collection number of MW BuA_MW_0001), specimens R2–R5.

Description. *Habitus.* Body (depending on preservation) ca. 0.31–0.45 mm long excluding terminal se-

tae, subparallel. Well sclerotised, with middle to dark brown cuticle. Head and thorax covered with short finger-shaped sensilla. Pair of long bristle-like setae inserted on posterior edge of thoracic segments and pair of long spiniform setae close to lateral edge of each postcephalic segment. Abdominal segments connected by soft membranous cuticle, resulting in varying length of abdomen;

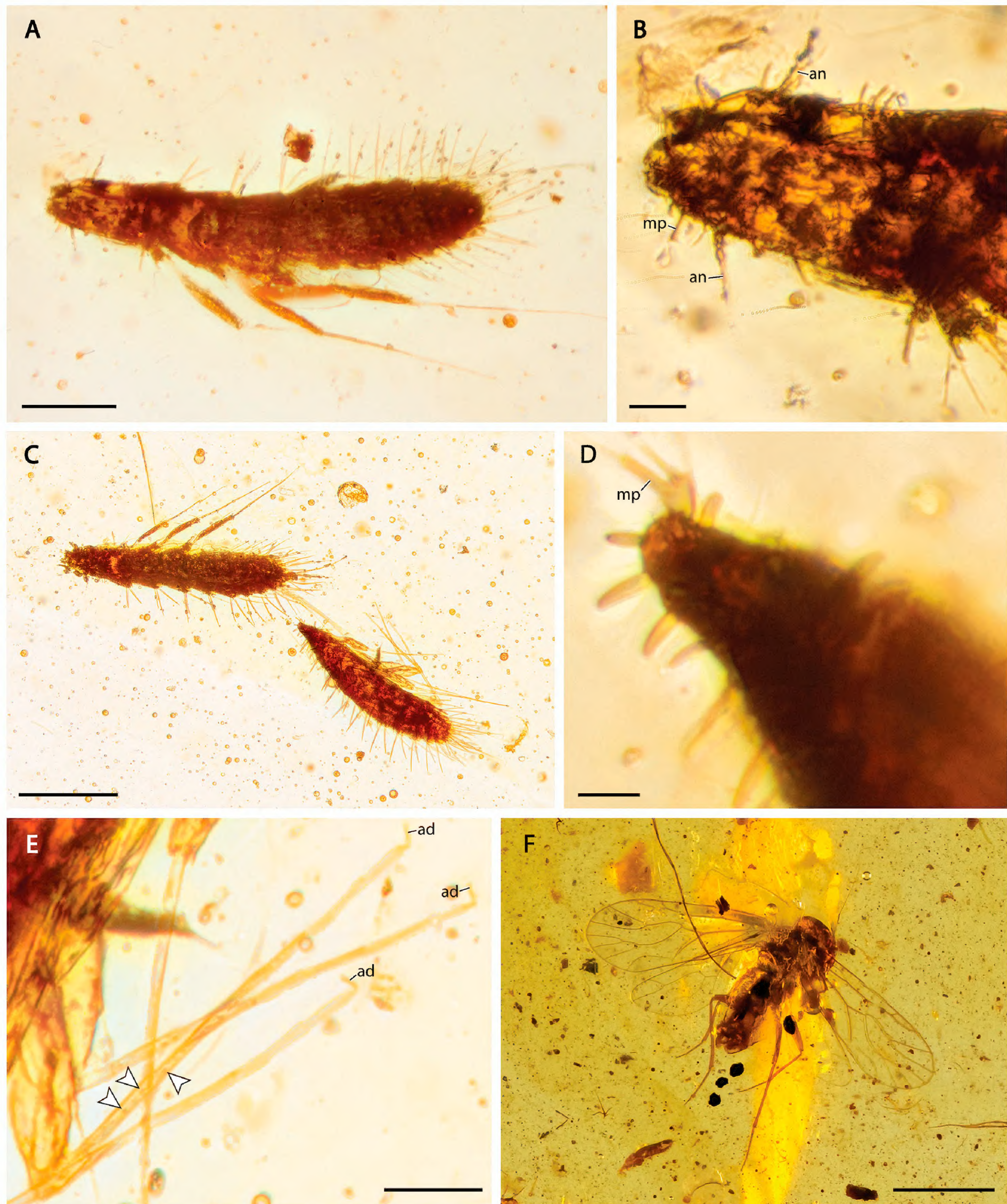


Figure 3. Detailed views of taxonomically important characters of *Ripidiini* larvae [R2–R5]. **A.** General overview of larva R2; **B.** Details of head of larva R2; **C.** General overview of larvae R3–4; **D.** Details of head of larva R4; **E.** Details of legs of larva R4; **F.** General overview of compsocid. ad = adhesive devices, an = antennae, mp = maxillary palps. Arrows in E indicate tibiotarsal setae. Scale bars: 100 µm (A); 20 µm (B); 200 µm (C); 10 µm (D); 50 µm (E); 1 mm (F).

abdominal segments I–III as long as mesothorax and metathorax combined. All three thoracic segments widest at posterior edge. Legs extremely prolonged; coxae cylindrical with one finger-shaped-sensillum and two bristle-like setae, and one long preapical bristle-like seta present on each femur; strongly elongated and thin tibiotarsus $1.3\text{--}1.7 \times$ as long as femur, with recognisable minute semierect spines, and with unpaired, flexible lobe-like

pretarsal attachment device. Abdominal segments IV–X with conspicuous concentration of long setae.

Head. Prognathous, elongated, rounded anteriorly, nearly parallel sided, very slightly widening posteriorly, with greatest width at hind margin; about half as long as pronotum, ca. $50\text{ }\mu\text{m}$ from anterior to posterolateral margin in dorsal view [R2], slightly less than $50\text{ }\mu\text{m}$ wide posteriorly [R2]. Stemmata or eye spots indiscernible.

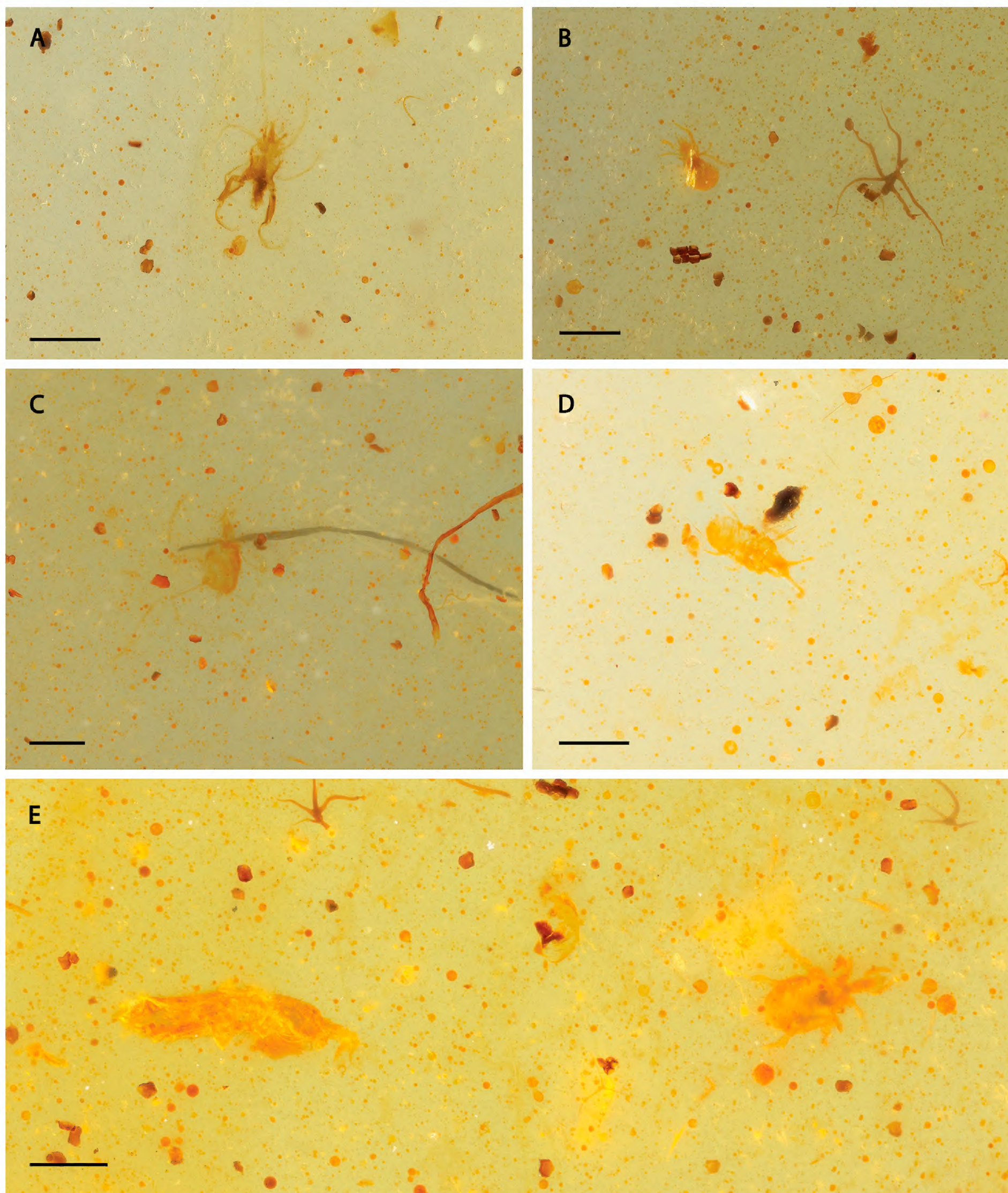


Figure 4. Detailed views of arthropod syninclusions [Ac1–Ac4, Co, Ny]. **A.** Unidentified mite Ac1; **B.** Oribatid (?) mite Ac2; **C.** Erythraeid mite Ac3; **D.** Nymph of hemimetabolous insect (?); **E.** Entomobryomorphan Collembola (left) and Erythraeid mite (right); Scale bars: $200\text{ }\mu\text{m}$ (A–E).

Transverse frontoclypeal strengthening ridge and dorsal ecdysial sutures (frontal sutures and coronal suture) not visible, probably absent. Posterodorsal edge slightly concave, overlapped by distinctly convex anterior pronotal margin. Scale- or lobe-like posterolateral extensions of head capsule absent. Posteroventral cephalic margin adjacent with anterior prosternal edge. Tentorial grooves not recognizable. Labrum not recognizable as

a separate structure, apparently fused with clypeofrons. Antennae at least two-segmented, situated in posterior half of head, consisting of one or two robust basal segments and bristle-like terminal seta. Mandibles robust, apparently movable, protruding in some specimens [R2], with curved outer margin; apices not overlapping each other when closed, mesal edges approximately parallel. Maxillary palpus long, with two segments visible,

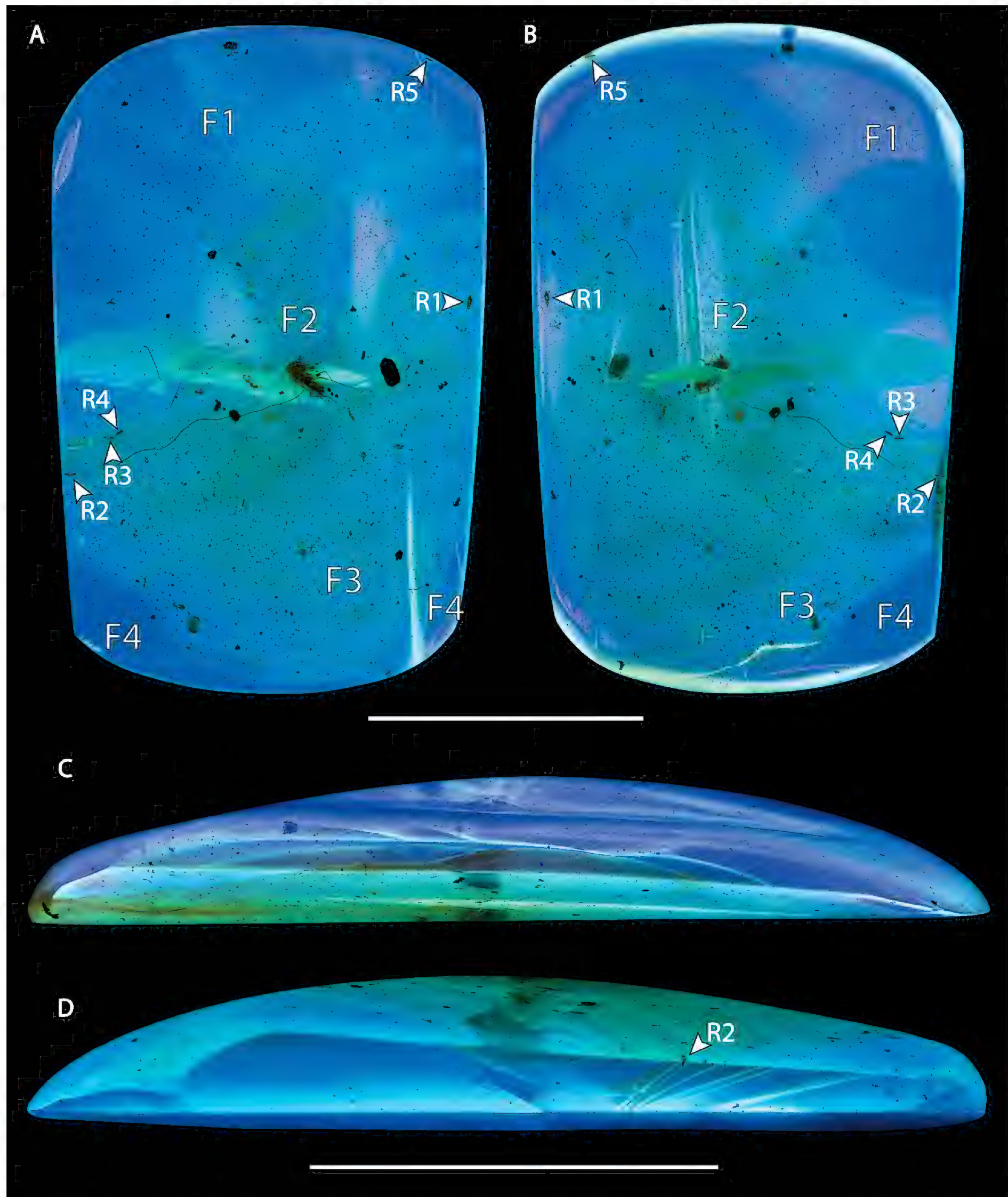


Figure 5. Kachin amber piece under one UV-light (368 nm wavelength). **A.** Side of amber piece where psocid is dorsal; **B.** Side of amber piece where psocid is ventral; **C.** Left long side of amber piece; **D.** Right long side of amber piece. R1 = Holotype of †“*Ripilarva*” *kachinensis* sp. nov., R2–R5 = Ripidiini larvae. Scale bars: 1 mm (A–D).

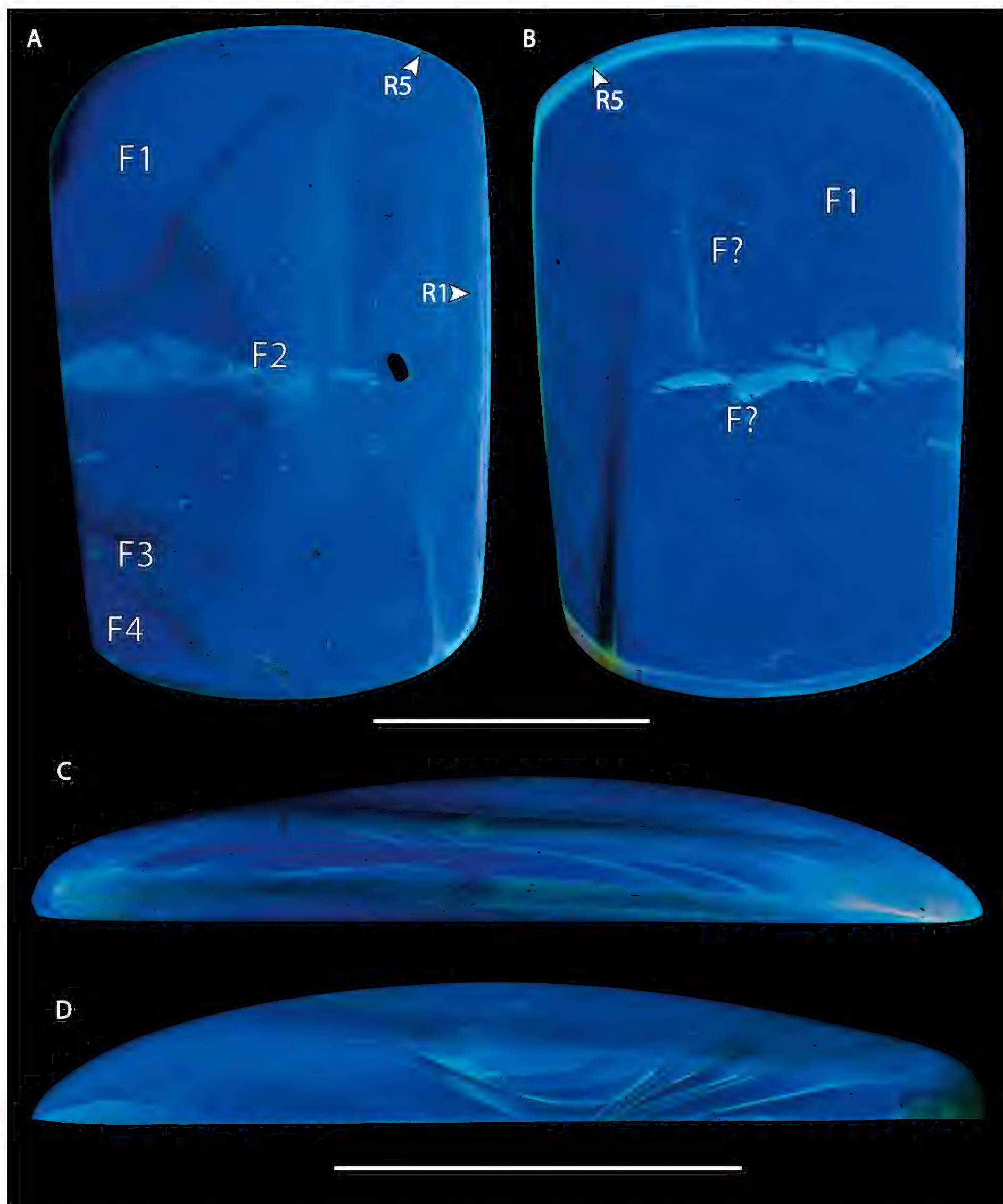


Figure 6. Kachin amber piece under two UV-lights (both with 368 nm wavelength). **A.** Side of amber piece where psocid is dorsal; **B.** Side of amber piece where psocid is ventral; **C.** Left long side of amber piece; **D.** Right long side of amber piece. R1 = Holotype of †“*Ripilarva*” *kachinensis* sp. nov., R2–R5 = Ripidiini larvae. Scale bars: 1 mm (A–D).

with one lateral and one terminal bristle-like seta [R4]. At least two pairs of finger-shaped sensilla present dorsally on anterior part of head, well projecting beyond cephalic edge [R2, R4].

Thorax. Prothorax longest and narrowest, metathorax shortest and widest [R2]. Pronotum well developed, mod-

erately widening posteriorly, with rounded posterolateral corners; anterior margin slightly convex, very slightly broader than posterior cephalic margin; distinct lateral edge absent; several pairs of erect finger-shaped sensilla placed close to lateral pronotal margin; two pairs of bristle-like setae placed at posterior edge of pronotum.

Prosternal ctenidia absent. Procoxae prominent, elongate, cone-shaped, inserted posterolaterally, very distinctly protruding beyond lateral pronotal margin, with pair of bristle like seta and one finger-shaped sensillum [R2]; trochanter indiscernible; femur strongly elongated (ca. 80 μm), slender, strongly narrowed basally, with very slightly convex hind margin, and one long preapical seta; tibiotarsus elongated (ca. 0.14 mm), about $1.75 \times$ longer than femur, very thin, strongly tapering distally, with several extremely small spines [R4]; pretarsal pad $1.5 \times$ longer than diameter of base of respective tibiotarsus, without other lateral projections or claws. Mesothorax distinctly shorter than prothorax, with anterior mesonotal corner overlapped by broadly rounded posterolateral pronotal edge and posterior corners widely rounded. Mesonotum simple, undivided, without median ecdysial line; finger-shaped sensilla placed close to posterior mesonotal edge; several pairs of bristle-like setae and finger-shaped sensilla placed along posterior margin. Sternal region without recognizable surface structures. Middle legs very similar to forelegs but even more elongated, total length 0.25 mm; mesocoxa similar in shape and size to procoxa, and similar preapical femoral seta and pretarsal pad present [R4]. Metathorax similar in shape to mesothorax. Metanotum slightly shorter than mesonotum. Hind legs very similar to middle legs.

Abdomen. Ten-segmented (ca. 0.2 mm [R2]), subparallel, slightly rounded laterally. Segments I–IV distinctly wider than remaining segments. Each segment with two pairs of erected long bristle-like setae at posterolateral corners and several setae on posterior edge, overlapping with each other (precise counting difficult). Ultimate segment rounded, without visible sucker or pygopod.

Measurements (mm). R2: length = 0.45, head and thorax combined = 0.25, head = 0.05, pronotum = 0.075, mesonotum = 0.07, metanotum = 0.55, abdomen = 0.2. R3: length = 0.42. R4 (shrunk and bent): length = 0.31.

Differential diagnosis. Species differs from *Blattivorus*, *Ripidius* and †*Paleoripiphorus* by distinctly prolonged pretarsal pads. Like *Blattivorus* and †*Paleoripiphorus* with slender head and thorax (much wider in *Ripidius*); like *Blattivorus* and *Ripidius* without prosternoctenidium (present in †*Paleoripiphorus*); antennae present (absent in †*Paleoripiphorus*). In its general morphology the larva is very similar to that of *Blattivorus*, also sharing long and thickened thoracic spiniform sensilla.

UV-Photography

At least 5 different resin flows are recognizable observing the amber piece from the flat side (Figs 5, 6A, B). The long sides indicate a relatively complicated structure of the amber, with several closely spaced resin flows (Figs 5, 6C, D). The results show that larvae R1–R4 are located in the same flow, while R5 is located in a different one. We define the specimens in the layer containing larvae R1–R4 as eusyninclusions, while R5 is a parasyninclusion.

Phylogenetic relationships

Analyses with NONA (Figs 7, 8) yielded between 4 and 24 trees of 30 steps (consistency index 0.83, retention index 0.91). TNT yielded 4 trees with the same length, and the same number was obtained after using the implied weighing option. In the strict consensus tree *Ptilophorus* and *Pelecotoma* were placed closest to the root of Ripiphoridae. The rest of the genera form a well-supported clade (branch support [bs] 5). Within this monophyletic unit all genera excluding *Ripiphorus* and *Macrosiagon* form a monophylum (bs 2). †“*Ripilarva*” is also confirmed as a clade (bs 2). Apomorphies and branch support values are shown in Fig. 7.

Discussion

Morphology of primary larvae

The minute primary larvae of Ripiphoridae are not only of great interest as highly specialised life forms, but are also a valuable source of phylogenetically relevant data complementing adult morphology (e.g., Švácha 1994; Batelka et al. 2022). The first instars of †“*Ripilarva*” are morphologically very distinctive. They share several distinctive features with primary larvae of Ripiphorinae and Ripidiinae, such as unsclerotised pretarsal pads and a cuticular surface covered by long bristle-like setae (notably on abdominal segments VIII and IX). However, they differ distinctly from larvae of all known extant Ripiphoridae by the presence of ctenidia on the head and thorax. The only exception is a similar prosternoctenidium in Cretaceous †*Paleoripiphorus*, but it is unclear whether these structures are homologous (Batelka et al. 2019). While the head of †“*Ripilarva*” *kachinensis* sp. nov., †“*Ripilarva*” sp. from Manitoba, and †“*Ripilarva*” sp. from Taimyr is conspicuously triangular, it is parabolic in †“*R.*” *parabolica* sp. nov. as illustrated in Beutel et al. (2016), similar to the condition found in Ripiphorinae. The bristle-like seta on both ultimate maxillary palpomeres of †“*R.*” *kachinensis* sp. nov. is similar to those observed in Ripidiini including †*Paleoripiphorus* (Batelka et al. 2019). Their “absence” in some †“*Ripilarva*” is likely due to observation constraints, as it is likely the case with the putative absence of trochanters in all †“*Ripilarva*”, sternal ctenidia in †“*Ripilarva*” from Manitoba, or metasternal ctenidia in †“*Ripilarva*” *kachinensis* sp. nov. Some structures may change their shape artificially in fossil larvae due to weak sclerotization. Abdominal segment X of †“*Ripilarva*” sp. from Taimyr, for instance, displays a knob-like shape, in contrast to the tubular one in all three remaining species. However, it is conceivable that this weakly sclerotised segment changes its shape when used for locomotion. The abdominal sucker in Ripiphorinae has similar characteristic and function (Tomlin and Miller 1989; Batelka and Straka 2011). All specimens of †“*Ripilarva*” display legs bent towards the head in almost identical orientation, a possible artifact caused by post-mortem contractions of muscles adapted for phoresy (Batelka et al. 2018).

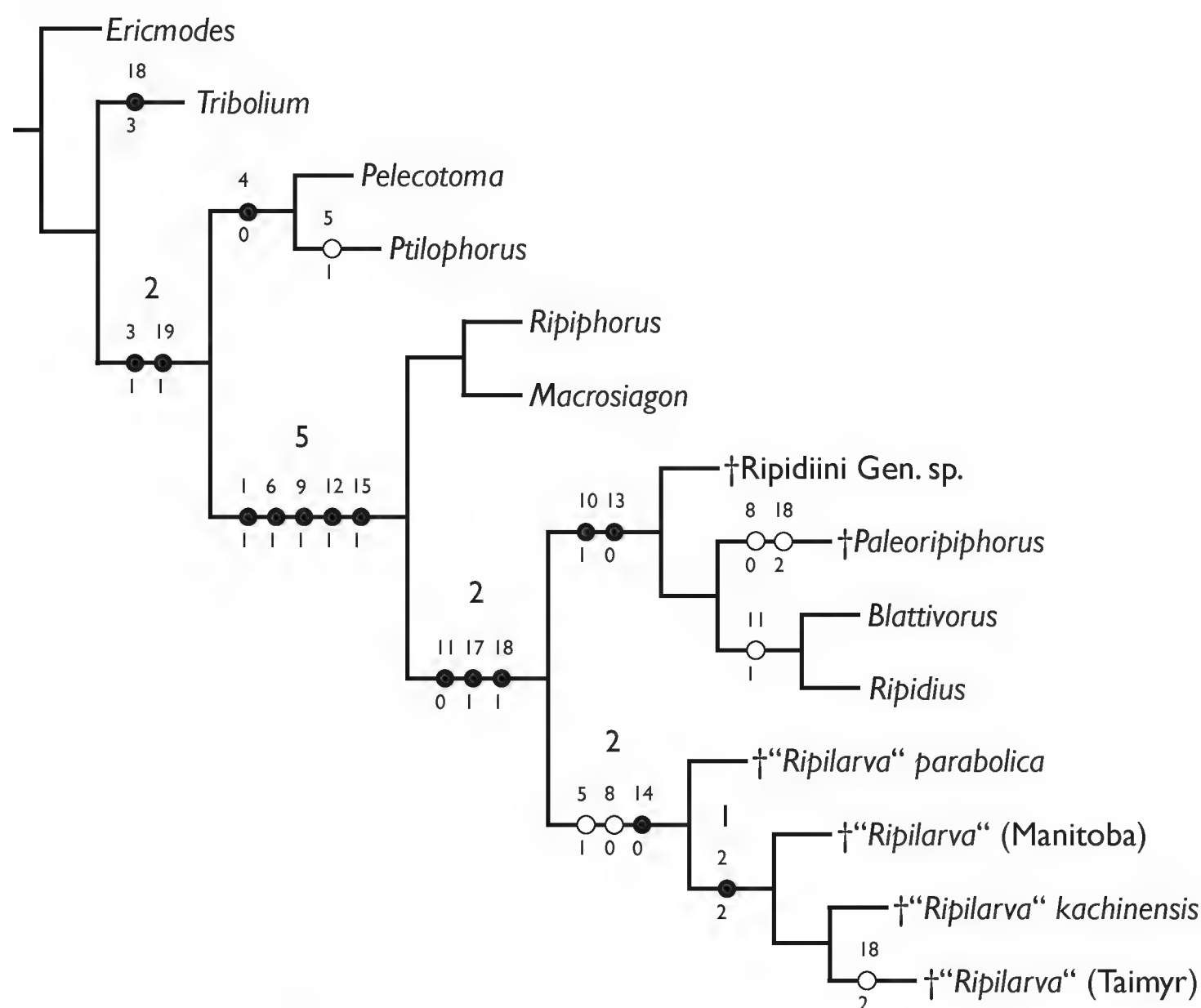


Figure 7. Cladogram obtained with NONA, apomorphies mapped on branches and branch support values above them. Full circles indicate non-homoplasious changes, homoplasious changes are marked by an asterisk in the following. Apomorphies: 3.1: dorsal ecdysial line absent; 19.1: urogomphi absent (Ripiphoridae); 4.0: lateral cranial area with scale-like sculpture (*Pelecotoma* + *Ptilophorus*); 1.1: triungulinid habitus, boat-shaped body; 6.1. antennal insertion posterolaterally; 9.1. meso- and metanotum distinctly widening posteriorly; 12.1. unpaired pretarsal adhesive lobe present; 15.1. abdomen widest in the area of segment 2, then continuously narrowing (Ripiphoridae excl. *Pelecotoma* + *Ptilophorus*); 11.0. Claws absent; 17.1. concentration of long setae on abdominal segments present; 18.1. segment X elongate and tube-like (Ripidiini incl. †“*Ripilarva*”); 10.1. tibiotarsus extremely thin and elongated; 13.1. pretarsal lobe minute (Ripidiini excl. †“*Ripilarva*”); 5.1*. eyes absent; 8.0*. ctenidia present; 14.0. secondary border between tibia and tarsus visible (“*Ripilarva*”); 2.2. head triangular and apically pointed (†“*Ripilarva*” excl. †“*Ripilarva*” *parabolica*).

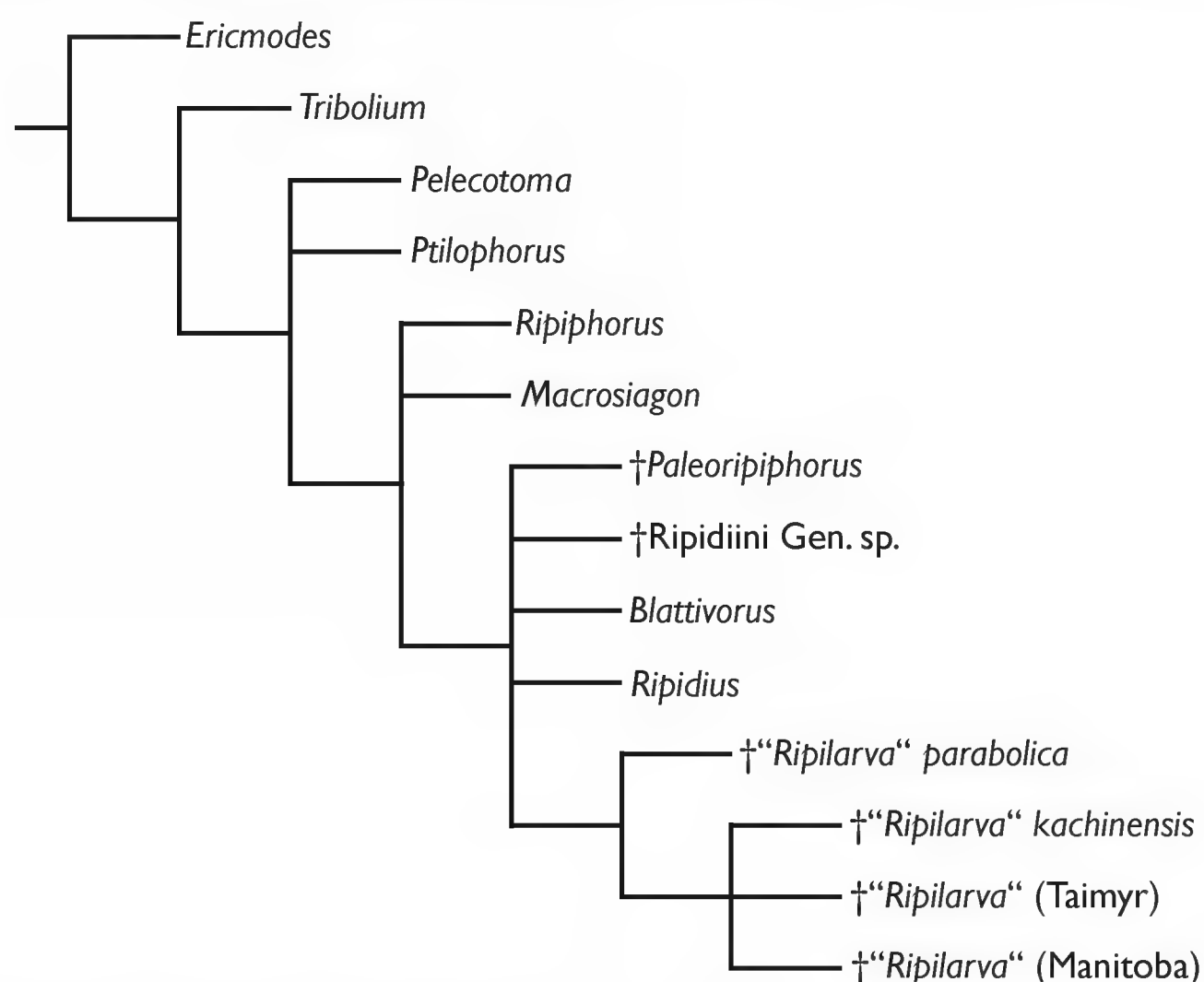


Figure 8. Strict consensus tree. Based on minimum length trees obtained with NONA (maximum parsimony).

Cretaceous invasive primary larvae of Ripidiini evolved a remarkable set of derived features. They developed various specialized structures involved in locomotion, such as lobe-like pretarsal attachment devices, microscopic spines on the prolonged tibiotarsus, and specialized setae and ctenidia on the body surface. It is likely that these unusual morphological features have evolved in the context of evolutionary arms races with their hosts. Considering that only larvae of four out of 24 extinct and extant genera are reliably documented (Batelka et al. 2019), it is premature to make conclusions about their evolutionary history. However, considering the fact that they are available in amber of various ages (sometimes with presumed conspecific adults) and larvae of extant species can be reared from eggs (Silvestri 1906; Riek 1955; Besuchet 1956), the group has a great potential to be among the best understood subgroups of Ripiphoridae. The larva of Ripidiini described in this study shares several features with some extant relatives. This includes similar arrangements of notal and abdominal spiniform setae, the configuration of the legs including unusual pretarsal pads, the shape of the mandibles, antennae and maxillary palpi, and a conspicuous body shape similar to *Blattivorus*. This Cretaceous morphotype thus provides evidence, that larvae of some extant lineages have acquired specialised features related with parasitism already 100 My ago. Barbier (1947) described sedentary behaviour for the female of *Ripidius pectinicornis*, an extant species of Ripidiini, allowing this species to spread worldwide (Falin 2001). The sedentary habit is likely for the Cretaceous species of Ripidiini due to their preserved morphological adaptations for this lifestyle. In contrast, a distinctive prosternotenidium and some other derived features of the larva of †*Paleoripiphorus* remain unknown in post Cretaceous taxa. The larva we described here thus represents another remarkable example of morphological stasis of some derived characters in this subfamily. This was documented previously based on uniflabellate antennae, reduced mouthparts and wing venation, enlarged compound eyes, and scale-like elytra in adult males of Cretaceous †*Amberocula* Batelka, Engel & Prokop, 2018, †*Cretaceoripidius* Falin & Engel, 2010, and †*Ripidinelia* Batelka & Prokop, 2019. The same applies to larviform bodies of females of †*Paleoripiphorus* (Batelka et al. 2021a).

Phylogeny

Our preliminary phylogenetic analyses of larval morphological characters reflect the results of a recent molecular study (Batelka et al. 2016) surprisingly well. *Pelecotoma* and *Ptilophorus* are placed closest to the root of the family. The sister group relationship between the two genera (Batelka et al. 2022) is not unambiguously confirmed, but suggested by an unusual potential synapomorphy, a lateral cephalic area with a scale-like surface structure (char. 4.1.). The monophyly of Ripiphoridae excl. *Pelecotoma* and *Ptilophorus* is strongly supported (branch support 5) by five unambiguous and unusual synapomorphies, notably a

boat-shaped body (char. 1.1), a posterolateral antennal insertion (char. 6.1), posteriorly widening meso- and meta-nota (9.1), unpaired pretarsal adhesive lobes (char. 12.1), and a characteristically shaped abdomen (char. 18.1). Ripidiini and †*Ripilarva* share three non-homoplasious synapomorphies, lacking claws (char. 11.0), a concentration of very long setae on the abdominal segments (char. 17.1), and an elongate and tube-like pygopodium (char. 18.1). †*Ripilarva* is supported by one non-homoplasious apomorphy, a tibiotarsus with a (secondarily) visible intrinsic border (char. 14.0), and two additional homoplasious derived features. A triangular and apically pointed head is a conspicuous apomorphy of †*Ripilarva* excl. †*Ripilarva parabolica*. Our data strongly suggest that †*Ripilarva* should be included in Ripidiinae.

Interpretation of the syninclusions

The piece of amber treated here raises the question of the circumstances of the embedding event. How accidental was the occurrence of two types of primary larvae of parasitic beetles in such a tiny space in a tropical Cretaceous forest? Ross (2024) reported 2,781 species from Kachin amber up to the end of 2023, and definitely many additional thousands of amber pieces were examined for biological inclusions since that time. Despite these intensive efforts, primary larvae of Ripiphoridae in any Cretaceous amber are only rarely reported (see Introduction). Moreover, previous studies have shown that the occurrence of †*Paleoripiphorus* is always subject to a certain pattern: they either appear in clusters up to several dozens of specimens or they co-occur with males or with both sexes of the same species (Batelka et al. 2019, 2021a). In contrast, conicocephalate larvae were always found isolated so far. Scientists usually handle polished and trimmed pieces, which means that most of them likely do not contain the entire fauna that they could have held originally. Therefore, the accidental occurrence of these short-lived life forms very close to each other appears highly unlikely.

It is evident from the state of preservation of the four larvae of Ripidiini that at least some of them were already dead (incomplete R5 and likely desiccated R4), while at least R2 was alive when rapidly covered by a flow of fresh resin. Fluid extruding from the mouth is visible, a phenomenon also observed in freshly killed primary larvae of another rhipiphorid, *Ptilophorus dufourii* (Batelka et al. 2022, fig. 4A). A different state of preservation in short-lived free instars (several days suggested by Besuchet (1956) for *Ripidius quadriceps*) is not surprising, as the same was reported for larvae and adults of †*Paleoripiphorus* in previous studies (e.g., Batelka et al. 2019).

Available data indicate that the mode of preservation of rhipiphorid first instars in amber is not accidental and that their taphonomy is affected by their bionomics. All known females of Ripidiini including Cretaceous †*Paleoripiphorus* are flightless and larviform. Pheromone communication of females of *Ripidius quadriceps* with restricted mobility, observed by Batelka et al. (2021b), is

very likely, similar to other extant and extinct species of this tribe. The cluster of four ripidiini larvae in the piece of amber treated here is likely the result of a behaviour of females similar to that documented for †*Paleoripiphorus* (Grimaldi et al. 2005; Batelka et al. 2019, 2021a). In clear contrast, the presence of a single specimen of †“*Ripilarva*” *kachinensis* sp. nov. corresponds with other isolated findings of similar larvae in Kachin amber, or amber from Manitoba and Taimyr. A likely mechanism explaining this rare co-occurrence with larvae of Ripidiini is a different reproductive behaviour of females. We suggest that more mobile females of †“*Ripilarva*” distributed relatively few eggs in a wide area, whereas sedentary females of contemporaneous Ripidiini deposited numerous eggs in a very confined site. This may have been related with the smaller size of females of †“*Ripilarva*” and the presence of wings. The shared preference for the same microhabitat and oviposition season might be explained by the same hosts used by both groups.

By comparing the amber piece under UV-light, we were able to distinguish several resin flows (Figs 5, 6A, B). It is likely that these occurred shortly after each other, as no noteworthy debris or air bubbles were trapped between the layers. It is evident that the larvae R1–R4 were trapped in the same flow of resin (Figs 5, 6A, B), but the larva R5 in another one. The placement of the specimens strongly suggests that these events occurred within a very limited time span. This conforms with our interpretation that the conicocephalate larvae and the larvae of Ripidiini occurred in the same microhabitat within a very narrow time window. Additionally, the psocid specimen is located at the transition zone between two flows and Schlabben are present around this insect. The preservation of the entire body is very uniform, without any noticeable differences between the anterior and posterior part, which are apparently trapped in two different flows. All ripiphorid larvae could therefore arguably be considered as eusyninclusions. However, as we use these terms as defined by Solórzano-Kraemer et al. (2023), we characterize the ripiphorid larvae R1–R4 as eusyninclusions, and larva R5 as a parasyninclusion. We consider the psocid (Fig. 1, Ps) to be part of the eusyninclusions as the main part of the body is trapped in the same resin flow as larvae R1–R4 (Figs 5, 6). Additionally, one erythraeid immature (Fig. 1, Ac4), the collembolan (Fig. 1, Co*), as well as the immature hemimetabolan (Fig. 1, Ny) are eusyninclusions. The oribatid mite (Fig. 1, Ac2), one mite of uncertain identity (Fig. 1, Ac1), and the second erythraeid immature (Fig. 1, Ac3) apparently belong to a single, different resin flow and are considered parasyninclusions (Figs 5, 6).

The entrapment of the psocid together with the ripiphorid larvae is likely accidental, as extant Comptosidae are known to inhabit tree trunks and bark microhabitats in rain forests (Mockford 1967; Mockford 2018). While the biology of the mites we observed in the amber is unknown, it is possible that both the ripiphorid larvae and the mite nymphs shared the same host. At least some erythraeid nymphs are ectoparasites of cockroach-

es (e.g., Southcott 1999; Muñoz-Cárdenas et al. 2015). This is tentatively suggested by the occurrence of both types of immatures in the same microhabitat in the same time period.

Conclusion

Our phylogenetic evaluation conforms to a recent molecular study (Batelka et al. 2016), with strongly supported clades Ripiphoridae excl. *Pelecotoma* and *Ptilophorus*, Ripidiini including †“*Ripilarva*”, and †“*Ripilarva*” excl. †“*Ripilarva*” *parabolica*. The presence of primary larvae of Ripidiini and †“*Ripilarva*” in a single piece of amber indicates that adults of both groups shared the same habitat and microhabitat, with the same timing of reproduction. However, the circumstances documented by all fossils described so far also suggest that the two ripiphorid groups probably employed different strategies to spread triungulinids at the locality. We assume that the females of Ripidiini were more or less sedentary and carried out oviposition at the same spot where they had previously left their host as the last larval instar. In contrast, the females of †“*Ripilarva*” might have been much more mobile, with a strategy of selective oviposition on multiple places, thus widely distributing the primary larvae.

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Author Contributions

J. Batelka designed the study, identified the larvae, and wrote the initial manuscript. J. Batelka and R. G. Beutel performed the phylogenetical analysis. M. Weingardt and B. L. Bock made photomicrographs and plates. All authors contributed to the writing and editing of the final manuscript.

Conflict of interest

The authors declare no conflict of interest.

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